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Shell Size Variation and Aggregation Behavior of *Littoraria flava* (Gastropoda: Littorinidae) on a Southeastern Brazilian Shore

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Abstract. *Littoraria flava* is a common snail on rocky shores and stems of mangrove trees along the southeastern coast of Brazil. However, studies on this species are absent. Our previous observation indicated a distance distribution pattern among shell size classes of this snail, depending on distance from the shore and occurrence in aggregation. We hypothesized that (1) snails with large shells would occur on tree stems far from the shore and (2) snails occurring in aggregation on rocky shores would be smaller than those occurring in isolation. We evaluated the effect of desiccation on the mortality of different size classes of snails experimentally submitted to a temperature of 40°C. We measured snail shells on 14 tree stems occurring in two mangrove strips (near and far from shore). Snails on tree stems of mangrove strips far from shore presented larger shells than snails near the shore. Snails in aggregations on rocky shores were smaller than isolated ones. The desiccation experiment showed that small snails (< 1 cm) lost water at a faster rate than larger ones (> 1.55 cm) and the mortality of small snails was above 70%. The distribution pattern of *L. flava* is probably related to differential shell size class tolerance to prolonged periods of emersion. Also, aggregation may be a behavioral mechanism to avoid water loss, as small snails are frequently found in aggregation and lose water at a faster rate.

INTRODUCTION

Shell size variation and aggregation behavior have been described for several marine gastropods (Feare, 1971; Butler, 1979; McQuaid, 1981; McCormack, 1982; Vermeij, 1973) including several species of the family Littorinidae, which occur on rocky shores (Underwood, 1979; Chapman, 1994, 1995; Chapman & Underwood, 1996; Chapman, 1997). However, similar records for Neotropical littorinids are scarce (Britton, 1992; Magalhães, in press).

In general, large shells may increase snails' reserve of water and provide resistance to desiccation and high temperatures more than smaller shells. Thus large snails can inhabit higher zones of the rocky shores, reducing the risk of dislodgement by waves (Vermeij, 1973).

Aggregations of snails may reduce the negative effects of desiccation and temperature (Garrity, 1984; Levings & Garrity, 1983), creating a moister microclimate. Aggregation may also allow snails to avoid displacement by waves (Boulding & Hay, 1993) or be the result of the presence of cavities or depressions, which are usually occupied by snails (Chapman & Underwood, 1996). Cavities and depression on rocky shores may protect the snails against physical displacement by waves, and retain moisture.

In this work, we have described, for the first time for the Neotropics, the variation in the shell size and aggregation behavior of *Littoraria flava* King & Broderip, 1832, found in the zone among tides of rocky shores and on mangrove tree stems along the south coast of the State of São Paulo, southeast Brazil. We tested the following hypotheses: (1) snails with the largest shell lengths occur on the highest zone on the tree stems, whereas the smaller ones occur on the lowest zone, and (2) snails that occur on trees established in areas nearer to the tide line and at a lower elevation (i.e., those that are submerged first) are smaller then those occurring on distant trees at a higher elevation.

Aggregations of *L. flava* are very common on shores along the southeast coast of São Paulo State. Our previous observations suggested that the snails with smaller shells (< 1 cm in length) occupied the center of the aggregate, and those with very large shells (> 1.4 cm) remained isolated. We only observed aggregation during periods of low tide. We therefore tested the hypothesis that (3) snails occupying the center are, on average, smaller than those on the periphery, and that (4) the average shell size of snails within the aggregates is smaller than the average shell size of isolated snails. Finally, we evaluated the effect of temperature on water loss and mortality of snails of different shell size classes in a controlled laboratory experiment. We expected that (5) small snails, under high temperatures (> 40°C) would lose water at a faster rate than the larger snails, resulting in a higher mortality rate.

MATERIALS AND METHODS

Study Area

This study was conducted at Araçá Beach (23°45′S, 45°30′W), São Sebastião, on the southern coast of the State of São Paulo, Brazil, during June 1997. The beach is sheltered from wave action, due to the presence of a small island known locally as Pernambuco Island. The distance between the island and the mainland is about 250 m with a topographical variation of 1.30 m. Contiguous to the island there is a small mangrove strip, formed mainly by the tree species *Rhizophora mangle* and *Laguncularia racemosa*. Another strip is situated near the continent, about 200 m from the first. *Littoraria flava* occurred on a rocky shore of the island and on the tree stems of the two mangrove strips. This study was carried out both on the island and along the mangrove strips, from 7–11 a.m. and with 0–0.2 m of tide.

Variation of *Littoraria flava* Shell Size on the Trees

To evaluate the vertical variation in snail shell size on the mangrove trees (hypothesis 1), we measured shell length (spire length) and height of each snail on the tree stem. In addition, we compared the average shell length of the snails occupying tree stems between two mangrove strips (near and far from the tide line) (hypothesis 2). For each strip, we measured all the snails located on the stem of 14 trees and calculated a mean of the shell size for each tree between habitats. In order to test for a possible variation of shell shape (e.g., elongated or globular) as described for other species of littorinids (Chapman, 1995), we measured the difference in the relationship between shell length and shell aperture for *L. flava* on trees and shore.

Shell Size Variation in the Aggregates

To test the hypothesis that the snails established in the center of aggregations are smaller than those occurring at the edges (hypothesis 3), we measured the shell length of snails in aggregations located on the rocky shore of Pernambuco Island. We chose aggregates with circular form (12–20 snails/aggregates) that were established outside of rock cavities or depressions. We measured all of the central snails (those that were surrounded by other member of the aggregations on every side) and all of those at the edges (delimiting the aggregation).

To evaluate whether the average size of the isolated snails was bigger than those in aggregations (hypothesis 4), we selected all isolated snails occurring in a radius of 50 cm around each aggregate. A snail was considered isolated if there was a minimum distance of 5 cm between it and any other snail.

Statistical comparisons of all hypotheses were made with Student t-test. The assumption of normality was tested graphically, and homogeneity of the variances was checked with Bartlett's test (Zar, 1984).

Desiccation and Mortality of Different Size Class Snails under Higher Temperature

To test the hypothesis that small snails (< 1 cm) suffer higher desiccation and mortality rates than the intermediate (1.30–1.45 cm) and large sizes (> 1.55 cm), we subjected 10 snails from each size class to a temperature of 40°C inside a stove. The exposure period was 4 hours. In order to keep each snail isolated during the experiments, we enveloped each one with a pierced cotton tissue (tulle). We weighed all snails before the beginning of the experiment and after its completion. The difference between the weight of the two measurements allowed us to estimate the water loss suffered by the snails and express it as a percentage. After the end of each experiment, we noted the number of dead snails in each size class to evaluate the relationship between the mortality and the shell size. The snails were put on the center of Petri dishes wet with seawater, and we considered dead those that did not show any movement after a period of 12 hours.

Voucher specimens were deposited in the Natural History Museum of the Universidade Estadual de Campinas, São Paulo, Brazil.

RESULTS

Littoraria flava were abundant on both the mangrove trees and the rocky island shore. The aggregates were common on the rocky shore, but absent on the tree stems. Field observations suggest that the aggregation was maximal during the low tide and especially when there was direct sun over the shore. The temperatures of the rock surface and of the air were around 24–26°C in the early morning (7–8 a.m.), but were higher than 30°C by midday. On rainy or cloudy days the aggregates on the rocky shore were smaller and less frequent.

The relationship between the shell aperture and its length indicated that *L. flava* did not show variation in shape between snails occurring on the rocky shore and on tree stems of different mangrove strips (Figure 1).

The average size of 778 snails sampled was 1.24 ± 0.21 cm (mean ± SD, range: 0.63–1.88 cm). The size of the snails' shells did not vary as a function of their height on tree stems (hypothesis 1) ($r = 0.11$, $p > 0.05$, $n = 397$). On the other hand, the snails occurring on mangrove trees distant from the tide line and therefore possibly subjected to a more extended emersion period (hypothesis 2), were bigger (1.30 ± 0.09) compared to those on the trees nearer to the tide line (1.19 ± 0.09, $t = -3.02$; $n = 14$; $p < 0.01$).

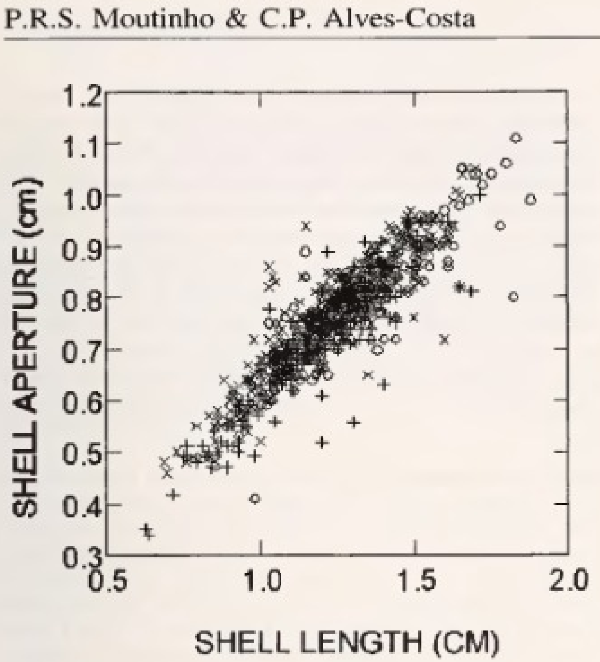

Figure 1

Relationship between shell aperture and shell length in snails (n = 778), *Littoraria flava*, occurring on rocky shore (×) and on tree stems of two mangrove strips near (+) and far (○) from shore in Araçá beach, São Sebastião, São Paulo State, Brazil.

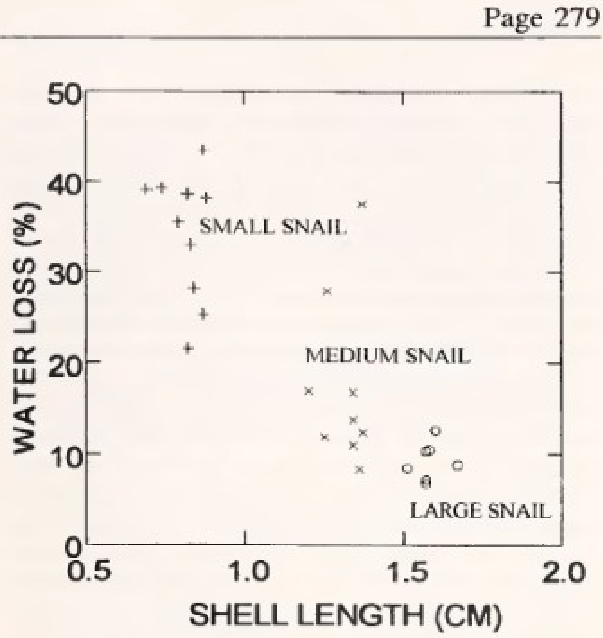

Figure 2

Relationship between water loss and shell length in snails *Littoraria flava* submitted to desiccation in a stove under 40°C, during 4 hours.

Snails occupying the center of the aggregations were smaller (1.15 ± 0.08 cm) than those at the edges (1.25 ± 0.05 cm, n = 11, t = 3.4, $p < 0.01$) (hypothesis 3). Snails in aggregations were smaller (1.21 ± 0.05 cm, n = 11) than isolated snails (1.30 ± 0.05 cm, n = 6, t = −2.9, $p < 0.01$) (hypothesis 4).

The experiment on the effect of temperature on the snails' desiccation indicated an inverse relationship between shell length and the percentage of water loss (Figure 2). After 4 hours in the stove, small snails (<1 cm) lost 40% to 60% of their original water content (before desiccating), and had a mortality rate over 70%. The medium-sized snails (1.30–1.45 cm) lost 5% to 35% of water, and had a mortality rate of less than 10%. This also held true for the large snails (> 1.50 cm) that lost less than 10% of water (Figure 2).

DISCUSSION

A vertical gradient in the distribution of the sizes can often be detected in a shore, with larger snails occupying higher zones, and smaller ones the lower zones (Underwood, 1979). Apparently, larger snails are better able to endure the stress resulting from prolonged periods of emersion (Vermeij, 1973; McMahon, 1990). On the other hand, variation in size can also be the result of differences in habitat conditions or the presence of cavities and other organisms. For instance, Chapman (1994) found that size of the shell in *Littorina unifasciata* is a function of its occurence on the shore possibly determined by rock inclination or the presence of cavities on its surface as well as the presence of barnacles. In this study, we did not verify the variation in the size of *L. flava* on the rocky shore. We judged this shore too narrow to produce a sharp gradient of shell size distribution as a function of the height of the shore. However, we could evaluate the existence of this gradient by relating the size with the height of the snails on the mangrove trees and also by comparing the size of the snails between the two strips of mangroves.

The absence of a relationship between shell size and the height of the occurrence of the snails on the stems, however, suggests that some conditions (moisture content along the stem, availability of food, and well-protected habitat) may serve to protect the snails from physical factors. Desiccation, high temperature, and wind normally promote spatial segregation of snails by different shell sizes on the rocky shores (Vermeij, 1973). On the other hand, there was a sharp difference in the average size of the snails between the two mangrove strips, suggesting that there is a gradient in shell size related to wave exposure, as on the rocky shores (Chapman, 1994). The larger snails occupied the mangrove strip distant from the tide line where the potential desiccation is higher due to long periods of exposure.

L. flava showed aggregation behavior only on the rocky shore, and not on tree stems. The aggregates can potentially confer advantages against predation and parasitism, and help snails to avoid dislodgement by waves and reduce the stress provoked by desiccation and high temperatures (Chapman & Underwood, 1996 and cited references). Normally, littorinids aggregate during low tides (Chapman, 1997) and occur in crevices in the rocks (Chapman & Underwood, 1996). In this study, the same trend was observed for *L. flava*. Although not quantified, the aggregation pattern seemed less intense during rain events and overcast conditions, which indicates the influence of temperature and desiccation as determinants for aggregation. Also, the effect of temperature and desiccation can determine patterns of aggregation and the spatial distribution of the shell size in *L. flava* in the aggregates, with large ones occurring isolated, and smaller ones occupying the center of the aggregates. Although the physiological tolerance to desiccation and high temperatures can differ among snails on the same shore, these factors are apparently more harmful to smaller snails than to larger ones, simply as a consequence of the ratio between area and volume of the shell, large for smaller snails. The experiments in a temperature-controlled stove confirm this hypothesis (4). The small snails were more susceptible to water loss and suffered higher mortality than the larger ones (Figure 2). Chapman & Underwood (1996) reported that *L. unifasciata* snails inside the aggregates held a greater quantity of water compared to isolated ones and that the aggregation was greater when the rocky substratum was dried. The size differences among the snails in the aggregates and the solitary ones found in this study suggest that the aggregation in *L. flava*, unlike that of *L. unifasciata* (Chapman & Underwood, 1996), is a behavioral response that reduces the stress induced by desiccation and temperature. Thus this behavior has a direct relationship with the size of the snails. This would explain, in part, the absence of aggregation in the snails that occur on tree stems, a substratum with supposedly higher humidity than the shore.

Although the evidence suggests that temperature and desiccation can be primary factors in promoting aggregation, especially among the smaller snails, it is possible that the size segregation among the snails is the result of the higher capability of dislocation of larger snails. Garrity & Levings (1984) observed that the activity period of the mollusk *Nerita scabricosta* during low tide was inversely related to the individual's shell length. The same was found for *Tegula funebralis* (Marchetti & Geller, 1987). Therefore, small snails cover shorter distances than larger ones and return first to crevices to form aggregations. Furthermore, smaller snails can occupy small gaps in rock crevices and among the larger snails, facilitating their occurrence in the aggregates. In any case, the aggregations may provide shelter to small snails, protecting those more vulnerable individuals from variations in physical conditions. Apart from the supposed advantages given by the formation of the aggregates, some field observations suggested an extra advantage of aggregation to smaller snails. In the field and in the lab (we packed together small and large snails in a glass pot), they were observed attached to the shells of larger snails and in continuous feeding activity. We sometimes found larger snails with the shells apparently "scraped," and in some, the layer of microalgae that normally covers the large shells of *L. flava* totally removed by the smaller snails. Once each shell became completely "clean," smaller snails were not observed on them anymore. Therefore, it is possible that the aggregates also provide an extra food resource available on the shells of larger snails. Use of the shells of larger snails as feeding substratum by the smaller ones may explain in part the maintenance of aggregates in *L. flava* and possibly in other littorinid species.

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